

THE RELATIONSHIP OF REPRODUCTIVE TEMPERATURE AND THE GEOGRAPHICAL RANGE OF THE MARINE WOODBORER LIMNORIA TRIPUNCTATA¹

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The objective of the study was to determine the influence of temperature on populations of the wood-destroying isopod *Limnoria*. The genus, which is economically important, contains about 16 described species (Menzies, 1957; Menzies and Becker, 1957; Pillay, 1957). Geographically, the species of the northern hemisphere have been divided into boreal, *L. lignorum*; temperate, *L. quadripunctata*; temperate-tropical, *L. tripunctata*; and tropical, 5-7 species.

The species we have worked with, *Limnoria tripunctata*, is found around the world. It is a hardy species which survives and reproduces under laboratory conditions. Our interest has been population growth at temperatures which might be encountered by the species in nature. On the basis of our results, we believe that we can explain the known distribution of the species in terms of the effect of temperature on population growth.

The specimens studied were collected through the courtesy of Mr. Thomas P. May, manager at the International Nickel Company testing laboratory at Wrightsville Beach, North Carolina, where the species is particularly abundant. The animals were air-shipped to the laboratory in containers which were packed so that oxygen was not excluded.

PROCEDURE

The animals received at the laboratory were removed from the infected wood, and sorted for size and sex. For each culture, 25 males and 25 non-gravid females were placed in a dish containing sea water and a piece of presoaked pine. In all three experiments a total of 1050 animals was used. Non-gravid females were selected in order to keep each culture equivalent to the next. The use of females with eggs in different stages of development would have permitted errors in defining the reproductive temperature range and population growth at the various temperatures. In order to permit the animals to establish burrows in the wood, each culture was allowed to stand one week at room temperature (20-24° C.). Salinity was held within tolerable limits by addition of distilled water. Tolerable limits, 30-39‰, were determined by preliminary experimentation. Salinity data for the three experiments are presented in Table I.

Seven cultures were prepared for each experiment in the manner described and one of each was put into a controlled temperature box and kept for a period of 66 days. This time duration was selected in order to allow for the production of young, but not their maturation. The cultures were kept at approximately

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0, 5, 10, 15, 20, 25 and 30° C. Usual temperature variation in the cultures was ± 1° C. Short-term larger variations did occur as a result of equipment and power failure. These occasional failures resulted in a gradual return to room temperatures. For over 99% of the time, temperature variation was within ± 1° C. The temperature means from the twice daily record are shown in Table I.

TABLE I
Salinity of culture water at the start and finish of each experiment

Original salinity	Experiment I June, July, Aug. 35.7‰	Experiment II Nov., Dec., Jan. 34.1‰	Experiment III May, June, July 35.0‰
Temperature		End salinities	
0°	37.0‰	34.2‰	34.5‰
5	36.8	34.1	33.7
10	37.2	34.0	33.6
15	37.9	33.6	35.1
20	38.1	33.8	33.8
25	37.6	33.8	33.2
30	38.4	32.5	34.6

Mean temperatures during each 66-day period

Experiment I June, July, Aug.	0.5° C.	5° C.	9.9° C.	15.1° C.	20° C.	25° C.	29.8° C.
Experiment II Nov., Dec., Jan.	0° C.	5° C.	10° C.	15.1° C.	20° C.	25.1° C.	29.9° C.
Experiment III May, June, July	1° C.	6° C.	11° C.	16° C.	21° C.	24° C.	29.5° C.

The measurements taken of the young at the end of the 66-day period are recorded in size class, based on pleotelson width. The size classes used were taken from Johnson and Menzies (1956).

RESULTS

The results of three experiments, each of 66 days duration, are presented in tabular form (Tables II and III). These are the number of young present at the end of each experiment, the largest size attained by the young, adult mortality and gravidity of surviving females. From these data the population change in 66 days has been determined (Fig. 1).

Cultures kept at 0° C. showed no reproduction and the highest adult mortality (86–100%). At 0° C. the animals were immobile, did not feed and starvation is the probable cause of death.

The 5° C. cultures also showed no reproduction and a high adult mortality (50–92%). The animals were feebly motile and showed slight feeding, but here again starvation is the probable cause of death.

The 10° C. cultures showed no reproduction and a lower mortality (0–64%).

In two experiments gravid females were present ; however, only eggs were found, and no larva or young were produced in the 66-day period. The animals were sluggish but did feed.

The 15° C. cultures showed a reproductive rate between 0 and 6 young produced per female. We are confident that a female produces more than one brood

TABLE II

Degrees Centigrade.....	0°	5°	10°	15°	20°	25°	30°
Adult mortality—Number of individuals in each culture of 50 animals that died in 66 days							
Experiment I June, July, Aug.	46	25	6	3	8	7	7
Experiment II Nov., Dec., Jan.	50	46	32	20	27	26	32
Experiment III May, June, July	43	28	0	4	2	0	32
Number of young present at the end of 66 days							
Experiment I June, July, Aug.	0	0	0	152	302	457	254
Experiment II Nov., Dec., Jan.	0	0	0	0	43	64	9
Experiment III May, June, July	0	0	0	20	45	73	0
Largest size class attained by young in 66 days*							
Experiment I June, July, Aug.	—	—	—	2	3	3	3
Experiment II Nov., Dec., Jan.	—	—	—	—	2	2	2
Experiment III May, June, July	—	—	—	2	3	3	—

* Pleotelson Width Size Classes after Johnson and Menzies (1956).

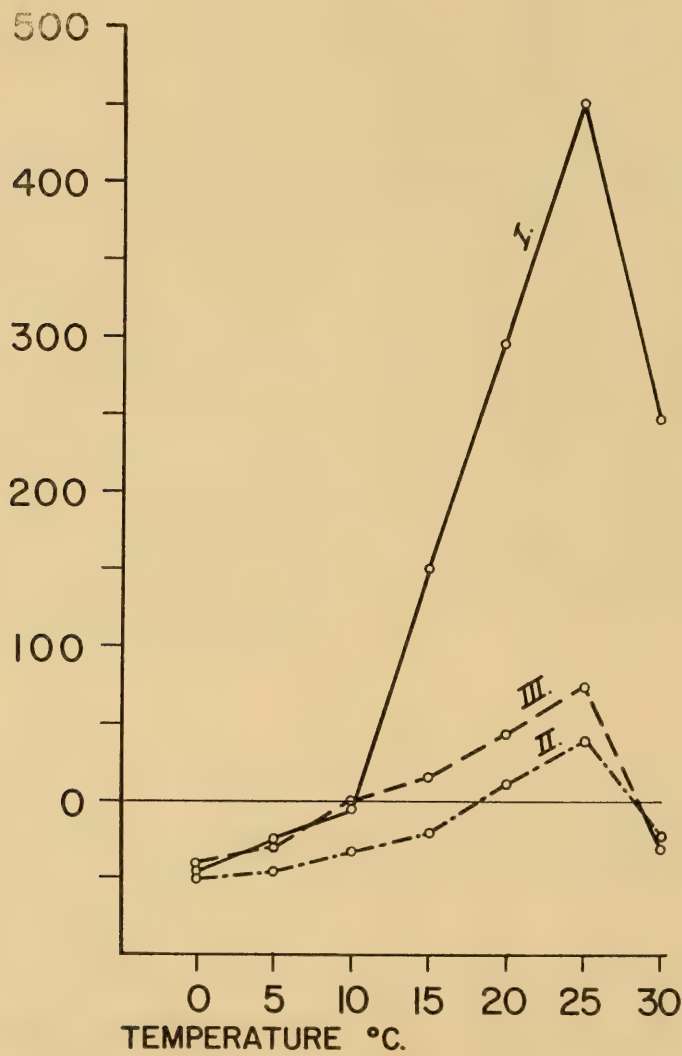
Class	Width in mm.
2	.28-.33
3	.35-.40

during her lifetime and therefore a 15° C. temperature permits population growth to occur. Adult mortality was 6-40%.

The 20° C. cultures showed a reproductive rate between 2 and 12 young per female. The average rate was 5 young per female and growing population is evident. Adult mortality varied between 4 and 54%.

TABLE III
Gravidity at the end of the experiments

Degrees C.	Experiment I June, July, Aug.			Experiment II Nov., Dec., Jan.			Experiment III May, June, July		
	No. females present	No. females gravid	Per cent gravid	No. females present	No. females gravid	Per cent gravid	No. females present	No. females gravid	Per cent gravid
0°	3	0	0	0	0	0	4	0	0
5°	9	3	33	1	0	0	12	0	0
10°	21	9	43	14	0	0	25	9	32
15°	16	9	56	16	0	0	22	1	5
20°	21	7	33	16	0	0	23	9	39
25°	22	7	32	18	1	6	25	9	32
30°	20	2	10	7	0	0	0	3	33



POPULATION CHANGE IN 66 DAYS

FIGURE 1. Population change at various temperatures after 66 days.

The 25° C. culture showed a reproductive rate between 3 and 18 young per female. The average rate was eight young per female, or about 1.6 times that of the 20° culture. The adult mortality rate was 0–52%.

The 30° C. culture showed a reproductive rate between 0.3 and 10 young per female. The average rate was three young per female. The adult mortality varied between 14 and 64%.

The most obvious feature of the three experiments is the lack of population growth below 10° C. The animals do not feed at these temperatures and eventually die of starvation as their fat reserve is depleted. The greatest population increase occurred in the cultures kept at 25° C. This might be considered the optimal temperature for population growth.

Adult mortality was highest at temperatures below 10° C. and at 30° C. Mawatari (1950) records 2–6° C. as the temperature lethal to adults of *Limnoria lignorum* (actually *L. tripunctata*). Our results also agree with the findings of Kampf (1957), who reports maximum population growth for *Limnoria tripunctata* from the Mediterranean to occur at 24° C. He also reports a shortening of the life span at higher temperatures which may account for the higher mortalities at 30° C.

INHERENT SEASONAL RHYTHM

Kampf (1957) reported a cyclic occurrence of gravidity for *Limnoria* kept under reasonably constant aquarium conditions. Unfortunately, his populations were mixed cultures of two species, *L. carinata* and *L. tripunctata*. Nevertheless, the low proportion of the former in his culture probably means that the cyclical record of gravidity is real for *L. tripunctata*. Coker (1923) reports that there is little winter gravidity found in Beaufort, North Carolina, *Limnoria* during the winter. Our observations of samples shipped from Wrightsville Beach, North Carolina, confirm this. The fact that culturing the specimens in the laboratory at temperatures approached only during the summer in the field still results in low gravidity and low young production suggests that we are dealing with an endogenous seasonal gravidity period which does not appear to be subject to immediate modification by change of temperature, and a reproductive rate imposed on the former which is subject to modification by change of temperature. It will be of the greatest interest to determine whether a seasonal endogenous reproductive period occurs in populations of the same species collected from a tropical locality where seasonal temperature fluctuations are almost absent.

DISTRIBUTION, TEMPERATURES AND POPULATION GROWTH

From the data presented, it would be a likely prediction that *Limnoria tripunctata* should not occur in localities where the sea water temperature is below 10° C. for most of the year. On the Atlantic coast the species is known to occur as far north as Cape Cod, Massachusetts. Here the yearly average sea water temperature is about 11° C. For five months of the year, however, the temperature rises above 15° C. and thus there is time for the populations to reproduce. The existence of the species is probably very precarious at this locality since monthly averages are below ten degrees for five months of the year. While signs

of *Limnoria* damage are extensive in the area, more often than not the burrows are empty and finding infested wood is sometimes a difficult job. North of Cape Cod, at Eastport, Maine, for example, the sea water temperature reaches 10°C . for only three months of the year. In such a situation we would not expect *Limnoria tripunctata* and to our knowledge the only species found there is *Limnoria lignorum*.

On the Pacific Coast of North America the species is not known as far north as Friday Harbor, Washington. Here the mean temperature of the surface sea water rises to $10\text{--}11^{\circ}\text{C}$. for only three months out of the year. During the re-

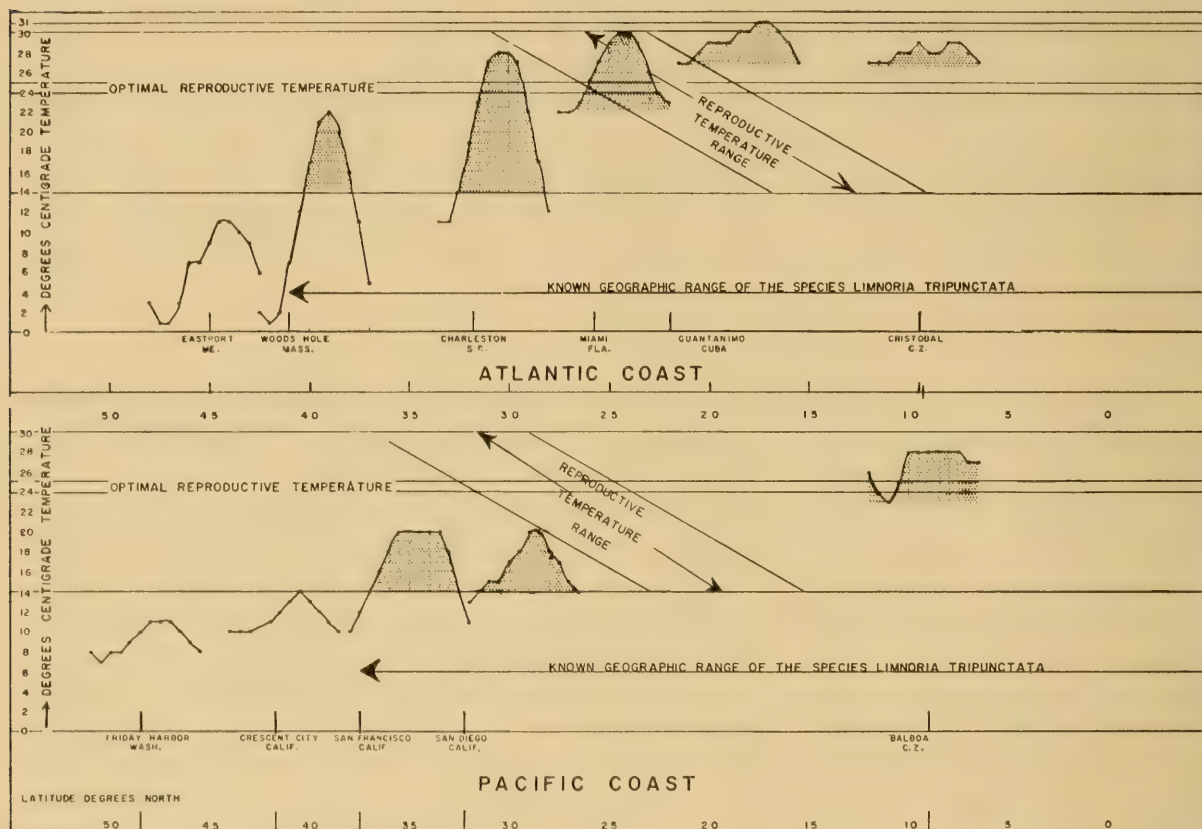


FIGURE 2. Geographical distribution, mean monthly surface sea water temperatures plotted at approximate longitude and reproductive temperature limits (the horizontal lines connected by the sloping block): The shaded areas represent the period of time that the temperature is within the reproductive range of the species. The minimum reproductive temperature, 14°C ., is estimated from the average of the three experiments to be at this temperature. At this point one young would be produced for each adult.

maining months it is lower than 10°C . This would give the species three months to feed, and no period of time suitable for reproduction. Southward, the species is also absent at Crescent City, California. Here temperatures rise above 10°C . for ten months of the year. The maximum temperature is 13°C . and this occurs for only two months of the year; 15°C . is not reached seasonally.

The species occurs along the Pacific Coast from San Francisco, California, to Mazatlan, Mexico, and probably as far south as Panama. At San Quentin, San Francisco Bay, lethal temperatures do not occur seasonally and temperatures favor-

ing population growth occur for seven consecutive months of the year. Seasonal temperature distribution, reproductive temperature limits for the species, and the established geographic distribution of *Limnoria tripunctata* in North America are shown in Figure 2. The remarkable coincidence between the geographic range of the species and the seasonal occurrence of temperatures favorable for reproduction leads us to conclude that temperature is a major factor controlling the distribution of the species.

The reason for the restriction of a species to a given geographic range has been of interest to zoologists and zoogeographers for many years. Temperature means, maxima and minima have been examined as parameters of possible control. The duration of a given range of temperatures has also been considered (Menzies and Hedgepeth, unpublished data). Experimentally determined physiological lethal limits for short periods of time are usually too wide to account precisely for the distribution of a marine species. Our examination of the effect of temperature on population growth of a single marine species suggests that the geographic distribution of this species is closely tied to the prevalence of temperatures favoring reproduction. The minimum duration of a favorable temperature necessary would depend on the growth rate of the species. Doubtless the duration of unfavorable temperatures for survival is also important. In terms of our experimental data it is difficult to explain the survival of populations of *Limnoria tripunctata* at Woods Hole, where it is necessary for the species to maintain itself for three months of the year at mean temperatures below 5° C. Our data suggest that this is a remote possibility; nevertheless, the species is precariously established.

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SUMMARY

1. Experimental results show that *Limnoria tripunctata* will feed at temperatures ranging from approximately 10° C. to 30° C. The reproductive temperature range appears to be from about 15° C. to 30° C. and the greatest population increase is in the neighborhood of 25° C. Excessive mortality results at 30° C.

2. Gravidity and hence number of young produced depends upon season and does not appear to be immediately modified by the presence of favorable reproductive temperatures.

3. The experimental results agree well with the known geographic range of the species.

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